EARTH SURFACE PROCESSES AND LANDFORMS
Earth Surf. Process. Landforms **45**, 2664–2674 (2020)

(wileyonlinelibrary.com) DOI: 10.1002/esp.4921

Influence of topographic, geomorphic, and hydrologic variables on beaver dam height and persistence in the intermountain western United States

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Received 8 October 2018; Revised 19 May 2020; Accepted 20 May 2020

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ESPL
Earth Surface Processes and Landforms

ABSTRACT: Stream ecosystems can be dramatically altered by dam-building activities of North American beaver (*Castor canadensis*). The extent to which beavers' ecosystem engineering alters riverscapes is driven by the density, longevity, and size (i.e. height and length) of the dams constructed. In comparison to the relative ubiquity of beaver dams on the landscape, there is a scarcity of data describing dam heights. We collected data describing dam height and dam condition (i.e. damaged or intact) of 500 beaver dams via rapid field survey, differentiating between primary and secondary dams and associating each dam with a beaver dam complex. With these data, we examined the influence of beaver dam type (primary/secondary), drainage area, streamflow, stream power, valley bottom width, and HUC12 watershed on beaver dam height with linear regression and the probability that a beaver dam was damaged with logistic regression. On average, primary dams were 0.46 m taller than secondary dams; 15% of observed dams were primary and 85% secondary. Dam type accounted for 21% of dam height variation (p <0.0001). Slope (p = 0.0107), discharge (p = 0.0029), and drainage area (p = 0.0399) also affected dam height, but each accounted for less than 3% of dam height variation. The average number of dams in a dam complex was 6.1 (SD ± 4.5) and ranged from 1 to 21. The watershed a beaver dam was located in accounted for the most variability (17.8%) in the probability that a beaver dam was damaged, which was greater than the variability explained by any multiple logistic regression model. These results indicate that temporally dynamic variables are important influencers of dam longevity and that beaver dam ecology is a primary factor influencing beaver dam height. © 2020 John Wiley & Sons, Ltd.

KEYWORDS: beaver; beaver dams; spatial analysis; ecogeomorphology; stream restoration

Introduction

On many landscapes in the western United States, North American beaver (*Castor canadensis*) alter riverscapes by building dams that pond and divert water as it flows overland and underground (Naiman *et al.*, 1988; Westbrook *et al.*, 2006; Pollock *et al.*, 2014). Increased water depth and decreased water velocity on beaver-impacted stream reaches (Stout *et al.*, 2017) often influence riparian ecosystems by curbing (or reversing) stream incision (Pollock *et al.*, 2014), influencing water table levels (Lowry, 1993; Westbrook *et al.*, 2006), altering baseflow (Majerova *et al.*, 2015; Puttock *et al.*, 2017), and increasing water temperature variability (Weber *et al.*, 2017). The magnitude of stream alteration and the potential ecosystem effects induced by a given dam are driven by its longevity and dimensions (Johnston and Naiman, 1990; Karran *et al.*, 2017). A larger, longer-lasting dam can impound more water, store more sediment, and influence adjacent groundwater tables to a greater degree than a smaller, short-lived dam at the same location (Naiman *et al.*, 1988; Burchsted *et al.*, 2010). Thus, the impacts of a beaver dam at a given location will vary according to the drivers of its size and longevity.

Due to their impacts on ecosystems, beavers, and structures mimicking beaver dams, are increasingly being implemented to restore riparian habitats, prompting the need for decision support tools to identify where such restoration practices are practical and what their potential effects on ecosystems may be (Pilliod *et al.*, 2018). Previous research has developed mathematical models to identify where beavers may build dams, and the densities of beaver dams that may be supported at specific locations (McComb *et al.*, 1990; Suzuki and McComb, 1998; Macfarlane *et al.*, 2017; Dittbrenner *et al.*, 2018). Such models utilize data describing ecologic, hydrologic, and geomorphic conditions of stream reaches to predict beaver dam occupancy and capacity (we refer to these models as dam suitability models, *sensu* Macfarlane *et al.*, 2017, hereafter). Dam suitability models for North American beaver have been applied at spatial scales ranging from ~100 km^2 (Suzuki and McComb, 1998) to over 200000 km^2 (Macfarlane *et al.*, 2017). In these models, average base flow, average peak flow, stream power, channel geometry (e.g. slope, width, depth), valley bottom width, and vegetation composition were identified as variables influencing beaver dam occupancy and capacity (McComb *et al.*, 1990; Persico and Meyer, 2009; Macfarlane *et al.*, 2017; Dittbrenner *et al.*, 2018). Essentially, dam suitability models link the characteristics of a stream reach to its ability to support beaver dams. In the context of beaver-based restoration, dam suitability models provide information about where beaver may build dams, but do not indicate the extent to which dams may potentially impact the riparian zone. To fully understand the potential impacts beaver dams (or structures mimicking beaver dams) may have on stream reaches, information describing the potential locations and densities of dams must be paired with information describing the size and duration of the structures.

The longevity of constructed beaver dams is highly variable and can range from less than a year (Demmer and Beschta, 2008) to several decades (Naiman *et al.*, 1988; Wright *et al.*, 2002). High streamflows often wash out or breach beaver dams (Demmer and Beschta, 2008). However, the effect of streamflow can vary greatly based on local conditions, where dams on confined or incised streams may experience higher wash-out rates (e.g. Demmer and Beschta, 2008) than unconfined, unincised streams (e.g. Lokteff *et al.*, 2013). The effect of streamflow on a beaver dam is determined by the structural integrity of the dam and the force exerted by flowing water on the dam (i.e. stream power). Thus, dam failure is influenced by the materials and methods used in dam construction, the magnitude of a flow event, and the characteristics of the channel on which the dam is located (Pollock *et al.*, 2015). Because stream power is influenced by many of the same variables that influence beaver dam location, there is reason to believe that the same variables used to describe channel dimensions and stream power in dam suitability models (e.g. Howard and Larson, 1985; Beier and Barrett, 1987; McComb *et al.*, 1990; Pollock *et al.*, 2004; Persico and Meyer, 2009; Macfarlane *et al.*, 2017; Dittbrenner *et al.*, 2018) may also influence beaver dam longevity over similar spatial extents.

The height of dams built by North American beaver generally ranges from 0.2 to 2.2 m, with mean height of about 1.0 m (Table 1). Occasionally, larger dams are observed (Dugmore, 1914; Gurnell, 1998), with some taller than 5 m (Grasse and Putnam, 1955). Dam lengths exhibit more variability, generally ranging from 0.5 to 308 m, with means between 16 and 69 m (Table 1); occasionally, dams greater than 700 m long are observed (Ives, 1942; Telegraph, 2010). Topographic and geomorphic variables that influence beaver dam occupancy and longevity may also influence the size (i.e. height and length) of beaver dams (Gurnell, 1998). For example, dam length will be constrained by channel width, or valley bottom width if the dam is built taller than the depth of the stream channel. Once beaver dams are taller than channel banks, dams must be built outward to contain overbank inundation, increasing the materials and effort needed to increase dam height, which introduces additional constraints to dam height and width. On steeper channels, a dam of a given height will inundate less area than a dam of the same height on a flatter channel. Despite these logical, expected relationships with geomorphic characteristics, few studies have examined the effects of topography on dam size, and only weak relationships between valley width, stream gradient, and beaver dam length and height have been reported to influence dam height and length (Beedle, 1991).

Beaver ecology may also affect dam height and longevity. Beavers build dams for three main purposes (Dugmore, 1914; Muller-Schwarze, 2011): (1) to inundate entrances to lodges and tunnels, providing shelter for the individuals of the colony maintaining the dams; (2) to inundate food caches that provide forage during winter months; and (3) to increase the colony's foraging range by providing additional inundated areas which serve as refuges from predators and corridors for transportation of food and building materials. The functional differences between dam types suggest that there may be height differences between them. For example, dams creating a pond that

Table 1. Summary of dam heights and dam lengths reported from studies examining multiple beaver dams constructed by North American beaver (*Castor canadensis*). Adapted from Beedle (1991). Note that studies examining single dams have reported dam heights over 5 m (Grasse and Putnam, 1955) and dam crest lengths longer than 700 m (Ives, 1942).

			Crest length (m)		Dam height (m)	
Author(s) (study location)	Year	Dam count	Mean	Range	Mean	Range
Karran *et al.* (Tierra del Fuego, Chile; Alberta, Canada; Minnesota, USA; Utah, USA)	2017	40	69	3–308	0.90[†]	0.2–2.0[†]
Majerova *et al.* (Utah, USA)	2015	10	–	–	1.00	–
Levine and Meyer (Montana, USA)	2014	4	–	10–36	–	1.4–1.7
Lokteff *et al.* (Utah, USA)	2013	21	–	–	0.99	0.3–2.0
Demmer and Beschta (Oregon, USA)	2008	–	8	<2.5–>25	0.80[†]	0.25–2.0[†]
Westbrook *et al.* (Colorado, USA)	2006	2	19	8–30	1.25	0.8–1.7
Meentemeyer and Butler, 1999 (Montana, USA)	1999	10	19	3–52	0.94	0.4–1.4
Beedle (Alaska, USA)	1991	44	32	2–132	0.70	0.5–1.5
McComb *et al.* (Oregon, USA)	1990	14	–	–	0.55	–
Bryant, 1983 (Alaska, USA)	1983	7	24	5–46	1.00	0.8–2.2
Townsend (Montana, USA)	1953	–	–	0.5–13	–	0.1–1.5
Smith, 1950 (Colorado, USA)	1950	30	27	–	–	–
Scheffer, 1938 (Washington, USA)	1938	23	13	2–37	0.94	0.3–2.1
Dugmore (Canada)	1914	–	–	91–152	–	–
Morgan, 1868 (Michigan, USA)	1868	9	19	–	–	0.3–1.5
Mean	**–**	**–**	**27.8**	**14–90**	**1.18**	**0.5–1.8**
Range	**–**	**–**	**13–69**	**0.5–308**	**0.55–1.25**	**0.1–2.2**
Total	**–**	**214+**	**–**	**–**	**–**	**–**

[†] Measure of maximum pond depth.

inundates a lodge or food cache (primary dams) may be larger because they must impound water deep enough to submerge certain features (e.g. lodge entrance, food cache). By contrast, dams that simply increase inundation area to allow beavers to access food and transport building materials (secondary dams), without leaving the relative safety of deep water, may be smaller.

Anecdotal evidence, and a few local dam height comparisons, suggest differences between the sizes of primary and secondary dams (Dugmore, 1914; Naiman *et al.*, 1988; Muller-Schwarze, 2011; Macfarlane *et al.*, 2017), but quantitative data describing differences between the sizes of primary and secondary dams are lacking. Additionally, while it is generally acknowledged that secondary dams occur more frequently than primary dams (Dugmore, 1914; Naiman *et al.*, 1988; Levine and Meyer, 2014; Macfarlane *et al.*, 2017), the ratio of secondary to primary dams has not been quantified at scales larger than a stream reach. Dam type may also be an important factor contributing to dam longevity. Because primary dams preserve food stores and/or inundate lodge entrances, they may be more likely to be immediately repaired following breaches (Dugmore, 1914). Over time, continued maintenance could lead to a greater ability of the dam to withstand potentially damaging flow events.

Many of the variables that are important predictors of where beavers may build dams, and how many dams they may build, may also be important to determine the height and longevity of constructed dams. However, to date, analyses relating the same geomorphic and hydrologic variables used in dam suitability models to beaver dam longevity and height at the landscape scale have not been conducted. While beaver dam suitability models inform restoration practices by identifying locations where beaver dams may be built, it is difficult to understand what the potential impacts of those dams may be in specific stream reaches or watersheds without understanding how beaver dam size and longevity vary at the same scales.

This study has two objectives aimed at quantifying the size and persistence of beaver dams and the variables that influence beaver dam size and persistence at the landscape scale. First, we identify and quantify differences between the height and occurrence of primary and secondary dams. Second, we identify and quantify the effects of topographic, geomorphic, and hydrologic variables on beaver dam height and persistence (i.e. the probability a dam is not damaged in a given year) at specific locations. We conduct field surveys to better quantify the size and condition of beaver dams at a broad spatial scale, and expect beaver dam height and persistence to vary as a function of dam type, channel gradient, stream power, stream flow, drainage area, and valley bottom width. The effects of individual variables and variable combinations are evaluated with linear (dam height) and logistic (dam persistence) regression. Greater knowledge of beaver dam longevity and dimensions, which drive the magnitude of a dam's impact, is essential to informing management decisions related to the effects of beaver dams (Pilliod *et al.*, 2018).

Methods

Study sites

We selected study sites in Utah and southern Idaho based primarily on presence of beaver and proximity to our research station, Utah State University (Figure 1). Study sites represented 11 HUC12 watersheds in southeast Idaho and throughout Utah that were located in the Middle Rocky Mountains, Basin and Range, and Colorado Plateau physiographic regions of the United States. Elevation of study sites ranged from 860 m (Santa Clara River) to 2380 m (Beaver Creek), and average annual precipitation ranged from 229 mm (Santa Clara River) to 1092 mm (Beaver Creek). Hydrographs at all study sites were characterized by a spring flood resulting from annual snow melt, followed by recession to baseflow in summer months. Estimated magnitude of the 2-year flood (Wilkowske *et al.*, 2008) on stream reaches where beaver dams occurred ranged from 0.26 to 26.71 cms (mean 2.71 cms) and baseflow (mean monthly flow for September) ranged from 0.002 to 0.74 cms (mean 0.08 cms). Beaver dams were located on stream reaches from high-elevation valleys where vegetation was composed primarily of sedges (*Carex spp.*), willows (*Salix spp.*), and aspen (*Populus tremuloides*), to a low-elevation, desert river (Santa Clara River) with vegetation composed primarily of cottonwoods (*Populus spp.*) and tamarisk (*Tamarix spp.*).

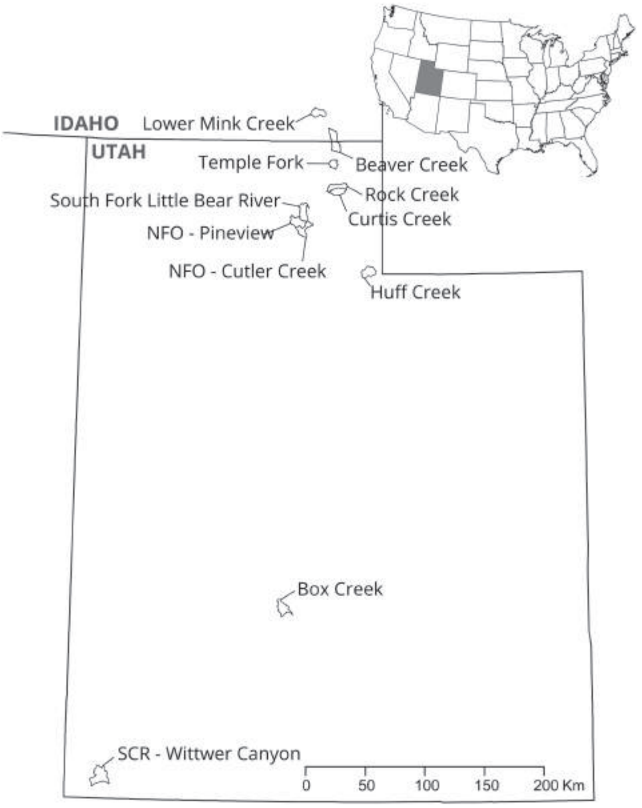

Figure 1. Utah and Idaho HUC12s where field data were collected via rapid field surveys. The North Fork of the Ogden River is abbreviated as NFO, and the Santa Clara River as SCR.

The lithology of watersheds surveyed in northern Utah and Southern Idaho was dominated by limestone, except for the North Fork of the Ogden River (Figure 1), which was comprised primarily of quartzite and poorly sorted, unconsolidated alluvium. The lithology of Box Creek is predominantly basalt; the Santa Clara River sandstone. All surveys were conducted in headwater HUC12 watersheds with drainage areas ranging from 41 km^2 (Temple Fork) to 110 km^2 (Beaver Creek), with the exception of the Santa Clara River which drains 1100 km^2 and has 12 upstream HUC12s. Two dams used for water storage and flood control are located upstream of the Santa Clara River study site. Water is only released from reservoirs via spillways once they have completely filled, cutting off the study reach from the majority of upstream flow (the reach contained flow when it was surveyed in September 2016).

Vegetation composition was similar in Temple Fork and Beaver Creek, with approximately 70% of the watershed covered by aspen or coniferous forest and 30% covered by sagebrush step. The Rock Creek, Curtis Creek, South Fork Little Bear River, Box Creek, and North Fork Ogden River watersheds had similar vegetation but were covered approximately evenly by forest and sagebrush. Huff Creek was comprised primarily of sagebrush (~70%) and aspen (~30%). The Santa Clara River was characterized by aspen and pine forest in the headwaters, which transitioned to pinyon–juniper–sagebrush communities, and finally to creosote and desert shrub communities around the study site.

Rapid field surveys

In the field, we visited beaver dam locations and collected data describing the location, height, type, condition, and construction material of each beaver dam via rapid assessments using iPads (e.g. Camp and Wheaton, 2014) equipped with field GIS software. Only perennial streams were surveyed. All surveys were conducted between 11 May and 22 September 2016, after peak runoff. Observers walked upstream along the stream until they observed a beaver dam. At each beaver dam, the observer recorded the dam height, dam type, dam condition, dam status, and the primary material used to construct the dam. Details for each recorded variable are presented in Table 2.

Dam heights were measured from the tallest point on the dam crest to the lowest point on the streambed downstream of the dam (Townsend, 1953; Beedle, 1991; Majerova *et al*., 2015). Dams that formed a pond where a beaver lodge or a food cache was located were classified as primary dams, all other dams were classified as secondary dams. Dam condition was classified as intact, breached, or blown out. Breached dams were dams where a partial removal or loss of material from the dam crest resulted in a lowering of the water surface in the pond. Blown-out dams were classified when enough of the dam was removed so that the dam no longer impounded water. Blowouts often occur without the complete removal of all the material comprising the dam (e.g. as in an end cut) and are often easily identified on the landscape many years after the blowout occurs (Burchsted *et al.*, 2010). Nevertheless, it is possible that some dams may have been completely washed out and not accounted for in our observations. In all, rapid field assessments were conducted for 500 beaver dams.

Beaver dam complex delineation

We defined beaver dam complexes as a single primary dam and all secondary dams spatially associated with the primary dam. Dam complexes were delineated using GIS software (QGIS 2.18) to attribute all dams associated with a complex, and dams of all conditions (intact, breached, and blown out) were included when delineating complexes. We considered all dams connected by backwater inundation (within approximately 10 m) to be a part of the same dam complex. Some complexes had beaver dams in parallel (i.e. on different anabranches or side channels), and these were considered part of the same complex when they were connected by either beaver-dug canals or the same backwater criterion above.

In most situations, dam complexes were clearly spatially segregated with obvious distance between the areas ponded by each complex, providing easy identification of which dams belong to which complex (Figure 2A). For cases where boundaries between complexes were not clearly defined, secondary dams were split between the complexes at a roughly equal distance between two primary dams (Figure 2B). In other instances, secondary dams did not exist in close proximity to a primary dam. Lack of primary dams may be attributed to several explanations (e.g. observers may not have detected lodges or food caches that were concealed by thick vegetation or murky water, beavers may dig tunnels and create lodges underground in streambanks instead of mounding mud and wood to create a lodge, observed dams may have been part of a dam complex that was under construction but not yet complete). In these cases, complexes were delineated by grouping secondary dams together according to the same criteria for complexes containing a primary dam (Figure 2C). We report the distribution parameters for the total number of dams in each dam complex, the number of intact dams per dam complex, and the number of damaged (blown out or breached) dams per dam complex.

Data analysis

Beaver dam height

We tested for differences in beaver dam height between primary and secondary dams with a *t*-test. We also modelled beaver dam height as a function of dam type (DT), channel slope (S), base flow (Q_{low}), flow of the 2-year flood (Q_2), stream power at base flow (Ω_{low}), stream power of the 2-year flood (Ω_2), upstream drainage area (DA), and valley bottom width (VB). Definitions for each variable and transformations that were applied to meet normality assumptions for linear regression are provided in Table 3. Slope, discharge, and stream power were calculated for 300 m stream reaches, following Macfarlane *et al*. (2017), using 10 m digital elevation models (DEMs) from the National Elevation Dataset. Discharge values were calculated from USGS regional equations (empirical, multiple-regression equations using gauge data) for Utah, which relate upstream drainage area to discharge (Wilkowske

Table 2. Variables collected during rapid beaver dam surveys, and value options for each variable. Surveys were conducted between 11 May and 22 September 2016.

Variable	Description	Values
Dam height	Measured from the top of the dam to the stream thalweg downstream of the dam	Continuous (m)
Dam type	Primary dams create a pond that inundates a lodge or a food cache	Categorical (primary, secondary)
Dam condition	The structural status of the dam	Categorical (intact, breached, blown out)
Dam status	Were beaver currently occupying or maintaining the dam?	Categorical (active, inactive)
Primary construction material	Material that was used most extensively in construction of the dam	Categorical (aspen, conifer, cottonwood, willow, riparian shrub, riparian tree, other shrub, other tree, sagebrush, grass, mud, rock)

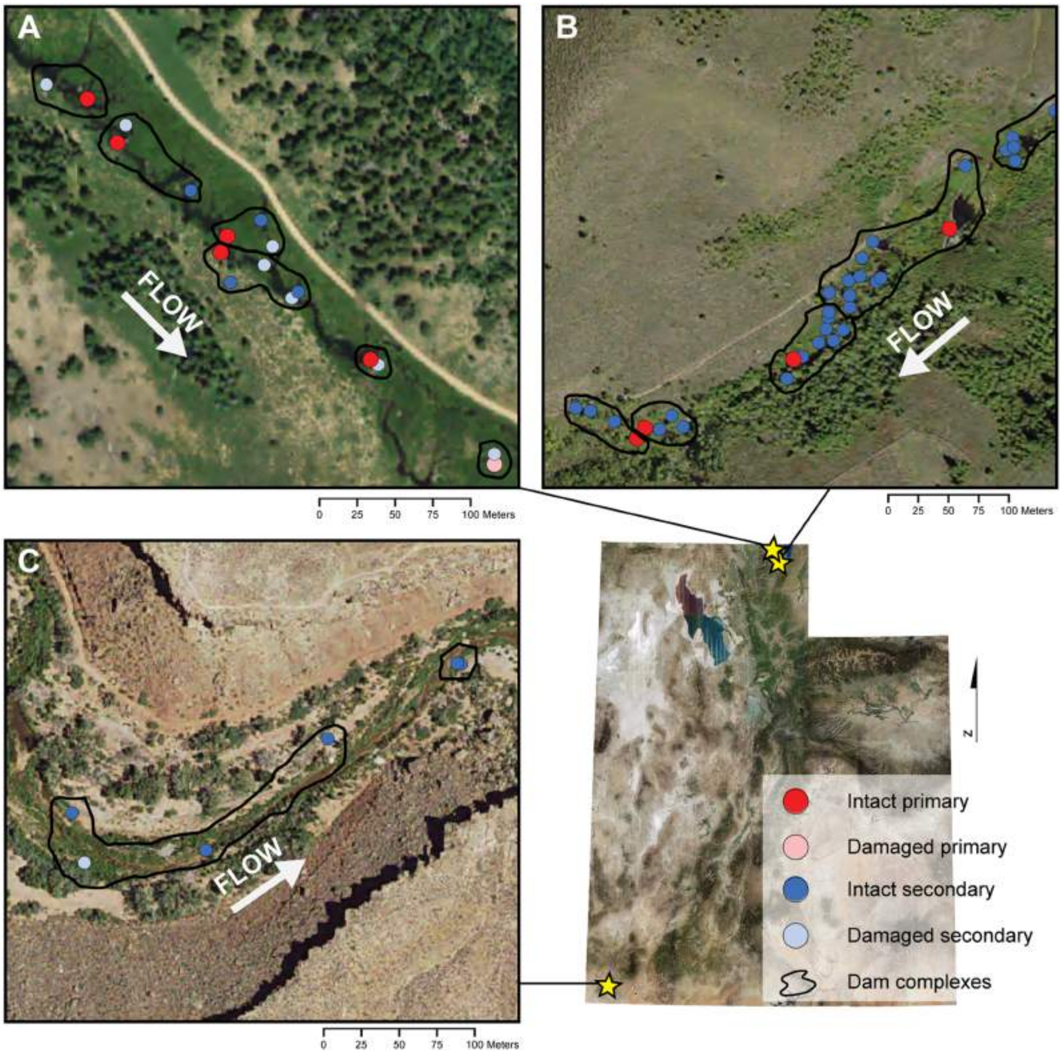

Figure 2. Examples of beaver dam complex delineation for complexes where (A) complex boundaries are relatively discrete, (B) complex boundaries are somewhat arbitrary, and (C) complexes do not contain primary dams. [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 2008). Ω_2 was calculated as the product of Q_2, S, gravity, and the density of water.

First-order linear regression models were created for each variable with dam height as the response variable. First-order models were assessed on Akaike information criterion (AIC), adjusted r^2, and *p*-value. Multiple regression models were also constructed to evaluate the effects of multiple variables on dam height. These models were evaluated on adjusted r^2 and difference in AIC adjusted for sample size (ΔAICc). We also calculated distribution parameters for the heights of all dams, primary dams, and secondary dams.

Probability of beaver dam damage

The odds of a beaver dam being damaged were modelled as a function of DT, S, Q_{low}, Q_2, Ω_{low}, Ω_2, DA, and VB with logistic regression. From aerial imagery collected by the National Agricultural Imagery Project (NAIP) during 2016, we determined if each dam was located on a single-channel (as opposed to a multi-channel) stream reach, and included this variable as ST. It is important to note that, from the data collected (i.e. single site visits), we were not able to determine when a dam was damaged and were not able to determine if dams were damaged weeks, months, or years before the survey. Thus, we

Table 3. Descriptions, transformations, and units of variables used in linear regression modelling of beaver dam height and logistic regression modelling of the probability a beaver dam was damaged.

Variable	Description	Transformation	Units
DT	Distinction between primary and secondary dams	–	–
S	Channel slope	log	%
Q_{low}	80% exceedance flow for the month of lowest discharge	log	$m^3 s^{-1}$
Q_2	Estimated discharge for a flood with an annual exceedance probability of 0.5	log	$m^3 s^{-1}$
Ω_{low}	Estimated stream power at Q_{low}	log	watts m^{-2}
Ω_2	Estimated stream power at Q_{50}	log	watts m^{-2}
DA	Upstream area draining to beaver dam location	log	km^2
VB	Width of valley bottom at beaver dam location	log	m
ST	Indicates if the dam was located on a single-channel reach	–	–
HUC12	The HUC12 watershed in which each dam was located	–	–

cannot accurately link dynamic variables (e.g. streamflow, annual climate) to the time dam damage occurred. Therefore, logistic regression models represent the probability that a beaver dam would incur damage based on the average characteristics of its location and not the specific characteristics of a day, month, or year.

The same definitions and transformations described in Table 3 were used for logistic regression analysis. First-order logistic regression models were created for each variable, with the log odds of a beaver dam being damaged as the response variable. A first-order model was also created for the HUC12 watershed each dam was located in. First-order models were assessed on AIC, McFadden's pseudo r^2 (Jackman, 2017), and *p*-value. Multiple logistic regression models were also constructed to evaluate the effects of multiple variables on the odds of the dam being damaged. Multiple regression models were evaluated on McFadden's pseudo r^2 (Jackman, 2017) and ΔAICc. HUC12 was not included in multiple logistic regression models, but was used to identify if conditions in HUC12 watersheds that were not captured by other covariates may have affected the probability of dam damage. All statistical analyses were conducted with R version 3.3.3 (R Core Team, 2017).

Results

Overall, we analysed data from 500 beaver dams collected via rapid field assessment (Table 4). Of the dams surveyed, 85% (n = 425) were secondary dams, and 15% (n = 75) were primary dams. As for dam condition, 65% (n = 325) of dams were intact, 19% (n = 94) breached, and 16% (n = 81) blown out. The majority of blown-out dams (n = 55) occurred in the Cutler Creek–North Fork Ogden River HUC12 (Table 4).

Beaver dam height

Heights of intact beaver dams ranged from 0.12 to 2.80 m and most closely followed a lognormal distribution (Figure 3). Primary dam heights ranged from 0.45 to 2.80 m and secondary dam heights ranged from 0.12 to 2.18 m. The distributions of primary and secondary dam heights were also lognormal (Figure 3). On average, the heights of primary dams were 0.46 m greater than secondary dams (t = 7.32, d.f. = 74, p <0.0001) and averaged 1.33 m in height with a standard deviation of

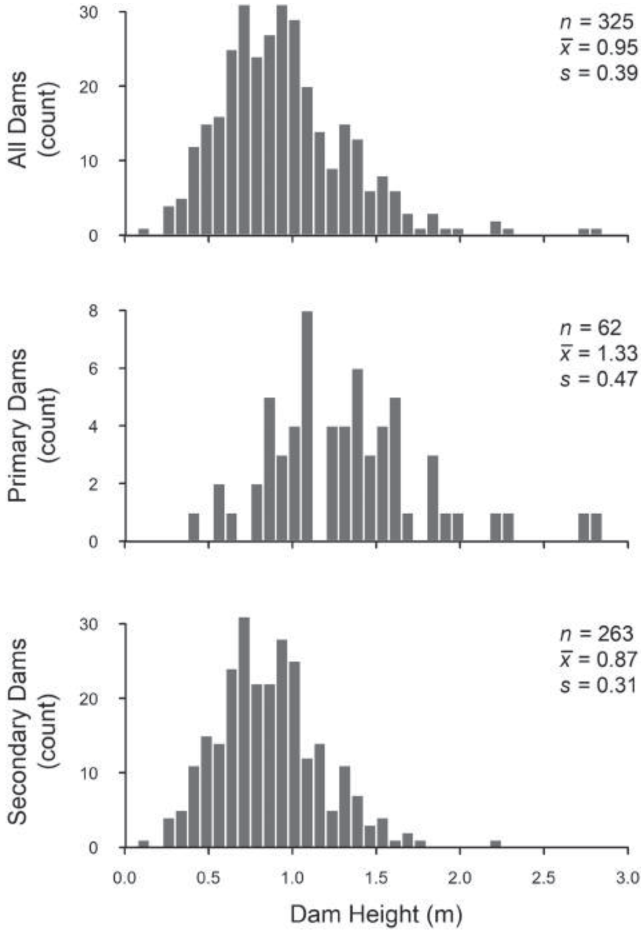

Figure 3. Dam height distributions of intact beaver dams for all dams, primary dams, and secondary dams collected in Utah and Idaho, USA between 11 May and 22 September 2016. The number of beaver dams (n), mean dam height ($\bar{x}$), and standard deviation of dam height (s) are reported for each dam type.

Table 4. Summary of the total number of dams for which rapid field assessments were conducted by 12-digit hydrologic unit (HUC12). H is the mean dam height for each HUC12 and SD the standard deviation of dam height. The total number of dams is also broken down by dam type – which includes primary (Prm) and secondary (Sec) dams, and dam condition – which includes intact (Intact), breached (Brchd), and Blown-out (Blwn) dams.

HUC12 name	H (m)	SD (m)	Prm dams	Sec dams	Intact dams	Brchd dams	Blwn dams	Total dams	Survey date(s)
Beaver Creek, Utah/Idaho	0.91	0.21	13	49	29	25	8	62	20 Jun 2016
Box Creek, Utah	0.77	0.23	4	17	8	8	5	21	1 Jul 2016
Curtis Creek, Utah	0.94	0.37	4	33	14	19	4	37	16 Jun 2016
Cutler Creek–North Fork Ogden River, Utah	0.88	0.28	8	78	30	1	55	86	12, 26 Jul 2016
Huff Creek, Utah	0.97	0.44	5	24	27	2	0	29	22 Aug 2016
Lower Mink Creek, Idaho	0.64	0.40	1	4	5	0	0	5	31 May 2016
Pineview Reservoir–North Fork Ogden River, Utah	1.01	0.35	7	15	20	2	0	22	13 Jul 2016
Rock Creek, Utah	0.92	0.28	9	93	79	21	2	102	7 Jun 2016
South Fork Little Bear River, Utah	0.88	0.24	1	8	9	0	0	9	7 Jul 2016
Temple Fork, Utah	1.08	0.52	22	95	96	15	6	117	11 May, 2 June 2016
Wittwer Canyon–Santa Clara River, Utah	0.58	0.19	1	9	8	1	1	10	22 Sep 2016
Total	–	–	**75**	**425**	**325**	**94**	**81**	**500**	
Average	**0.95**	**0.39**	–	–	–	–	–	–	

Table 5. Parameter effects, AIC, adjusted r^2 (Adj. r^2), and significance (*p*-value) for first-order linear regression models of dam height. DT = dam type, S = reach slope, Q_{low} = estimated baseflow discharge, Q_2 = estimated 2-year flood discharge, $\mathbf{\Omega}_{low}$ = stream power at estimated baseflow, $\mathbf{\Omega}_2$ = stream power at estimated 2-year flood discharge, DA = drainage area, VB = valley bottom width.

Parameter	Coefficient	AIC	Adj. r^2	*p*
DT secondary	−0.46	242.4	0.212	<0.0001
S	1.62	312.7	0.017	0.0107
Q_{low}	−0.01	320.5	0.003	0.7119
Q_2	−0.07	311.7	0.024	0.0029
$\mathbf{\Omega}_{low}$	0.03	317.5	0.006	0.0780
$\mathbf{\Omega}_2$	−0.03	319.8	0.000	0.3438
DA	−0.05	316.8	0.010	0.0399
VB	−0.08	317.1	0.008	0.0591

0.47 m, in comparison to secondary dams which averaged 0.87 m in height with a standard deviation of 0.31 m.

DT, S, Q_{50}, and DA all had statistically significant effects on dam height (Table 5). However, only DT (r^2 = 0.21) had an r^2 value greater than 0.05. The multiple regression model of dam height with the best performance included DT, Q_2, VB, and the interaction between DT and Q_2 (DT * Q_2) and explained 29% ($p < 0.0001$; Table 6) of variation in dam height. VB was not significant in the best-performing model, and the best model did not differ significantly from the same model with VB removed ($p = 0.11$). The five best-performing multiple regression models describing dam height are reported in Table 6.

Probability of beaver dam damage

DT, Q_{low}, $\mathbf{\Omega}_{low}$, ST, and HUC12 had significant effects on the odds of a beaver dam being damaged (Table 7). However, McFadden's pseudo r^2 (referred to as pseudo r^2 hereafter) was low (<0.1) for each variable. HUC12 accounted for 17.8% of variability in the log odds of a dam being damaged, followed by $\mathbf{\Omega}_{low}$, which explained 6.8% of the variability.

The best-performing multiple logistic regression model describing the odds of a beaver dam being damaged included DT and $\mathbf{\Omega}_{low}$ (Table 8). This model explained less variation (pseudo r^2 = 0.091) than HUC12 watershed (pseudo r^2 = 0.178), indicating that conditions unaccounted for by the assessed variables have greater effects on dam persistence. Other parameters that appeared in the five best-performing models were Q_{low} and interactions between DT and both $\mathbf{\Omega}_{low}$ and Q_{low}. However, none of these parameters had significant effects in their respective models (Table 8).

Beaver dam complexes

From the 500 surveyed beaver dams, we identified 82 beaver dam complexes. Dam complex size ranged from 1 dam to 21 dams, with a mean of 6.1 dams and standard deviation of 4.5 dams. The number of dams per dam complex most closely followed a lognormal distribution, with a mean of 4.7 dams and standard deviation of 2.0 dams (Figure 4). All 82 dam complexes contained at least one intact beaver dam and 53 complexes contained at least one damaged dam. The maximum number of intact dams in a single complex was 15, and the maximum number of damaged dams in a complex was 21.

Table 6. Parameter effects, adjusted r^2 (Adj. r^2), and significance (*p*-value) for linear regression models (top 5) describing beaver dam height, ranked by change in AIC adjusted for sample size (ΔAICc). DT = dam type, S = reach slope, Q_2 = estimated 2-year flood discharge, VB = valley bottom width.

Model	Parameters	Coefficients	*p*	Adj. r^2	ΔAICc
DT + Q_2 + VB + DT * Q_{50}	d.f. = 6		<0.0001	0.289	0.0
	Intercept	2.83	<0.0001		
	DT secondary	−1.67	<0.0001		
	Q_2	−0.31	<0.0001		
	VB	−0.06	0.1050		
	DT secondary * Q_2	0.30	<0.0001		
DT + Q_2 + DT * Q_{50}	d.f. = 5		<0.0001	0.285	0.6
	Intercept	2.64	<0.0001		
	DT secondary	−1.69	<0.0001		
	Q_2	−0.32	<0.0001		
	DT secondary * Q_2	0.30	<0.0001		
DT + Q_2 + S + DT * Q_{50}	d.f. = 6		<0.0001	0.283	2.6
	Intercept	2.64	<0.0001		
	DT secondary	−1.67	<0.0001		
	Q_2	0.32	<0.0001		
	S	0.01	0.7890		
	DT secondary * Q_2	0.30	<0.0001		
DT + S + VB + DT * S	d.f. = 6		<0.0001	0.265	10.7
	Intercept	2.37	<0.0001		
	DT secondary	−1.17	<0.0001		
	S	0.23	<0.0001		
	VBS	−0.08	0.0340		
	DT secondary * S	−0.23	0.0002		
DT + S + Q_2 + DT * S	d.f. = 6		<0.0001	0.264	11.4
	Intercept	2.20	<0.0001		
	DT secondary	−1.20	<0.0001		
	S	0.21	0.0002		
	Q_2	−0.05	0.0504		
	DT secondary * S	−0.23	0.0001		

Table 7. Parameter effects, AIC, McFadden's pseudo r^2 (Pseudo r^2), and significance (p-value) of first-order logistic regression models of the odds a beaver dam is damaged. DT = dam type (primary/secondary), S = reach slope, Q_{low} = estimated base flow discharge, Q_2 = estimated 2-year flood discharge, Ω_{low} = stream power at Q_{low}, Ω_2 = stream power at Q_2, DA = drainage area, VB = valley bottom width, ST = single-thread channel, and HUC12 watershed.

Parameter	Coefficient (log odds)	AIC	Pseudo r^2	p
DT secondary	1.11	640.9	0.022	0.0006
S	0.73	655.0	0.000	0.7664
Q_{low}	−0.70	625.9	0.045	<0.0001
Q_2	−0.03	655.0	0.000	0.7773
Ω_{low}	−0.48	610.6	0.068	<0.0001
Ω_2	−0.25	651.8	0.005	0.0722
DA	−0.04	654.9	0.000	0.6668
VB	−0.18	654.1	0.001	0.3161
ST	0.54	647.0	0.012	0.0045
HUC12		556.3	0.178	
Intercept	0.19			0.4468
Box Creek	0.29			0.5729
Curtis Creek	0.30			0.4762
Cutler Creek	0.43			0.2073
Huff Creek	−2.80			0.0003
Lower Mink Creek	−16.76			0.9875
Pineview	−2.50			0.0015
Rock Creek	−1.32			0.0001
South Fork Little Bear River	−16.76			0.9833
Temple Fork	−1.71			<0.0001
Wittwer Canyon	−1.58			0.0571

Discussion

With field observations of 500 beaver dams, we assessed variables influencing beaver dam height and the probability a beaver dam was damaged (i.e. breached or blown out). We also quantified the number and condition of beaver dams in beaver dam complexes, and the relative occurrence of primary and secondary dams. The results presented herein provide important information for implementation of beaver-based stream restoration and advancing scientific understanding and estimation of beaver dam size and impacts.

On average, primary dams were 0.46 m taller than secondary dams, and secondary dams were nearly six (5.67) times more prevalent than primary dams. These empirical data that describe the heights, and height differences, of beaver dams will be important for parameterization and calibration of tools (e.g. models) that estimate the potential impacts of beaver reintroduction to riverscapes. Additionally, these data provide a template to follow for mimicking the size and number of dams in beaver dam complexes during restoration implementation.

Dam type, which has been suggested to affect dam height but has not been previously quantified across multiple dam complexes (Dugmore, 1914; Macfarlane *et al.*, 2017), described the largest percentage of variation in dam height of all variables considered (21.2%). This finding indicates that beaver ecology, and not just physical variables describing the characteristics of a dam location, is an important factor affecting dam height. Additionally, the relationship between dam type and dam height may provide a (partial) explanation for why previous studies (e.g. Beedle, 1991) did not observe strong relationships between dam height and geomorphic variables. Primary dams are likely taller than secondary dams because they are built to create a pond large enough and deep enough to inundate food caches and entrances to lodge tunnels (Dugmore, 1914; Muller-Schwarze, 2011). In contrast, secondary dams may be built just tall enough to create the inundation extent and depth necessary for protection and to transport building materials, but occur more frequently than primary dams. Thus, when considering a stream reach with uniform geomorphic and hydraulic characteristics, a site occupied by beavers could generally be expected to have one tall (relatively) dam and several shorter dams.

Table 8. Parameter effects, McFadden's pseudo r^2 (Pseudo r^2), and significance (p-value) for logistic regression models (top 5) describing the odds of a beaver dam being damaged, ranked by change in AIC adjusted for sample size (ΔAICc). DT = dam type (primary/secondary), Q_{low} = estimated baseflow discharge, Ω_{low} = stream power at Q_{low}, DA = drainage area, VB = valley bottom width.

Model	Parameters	Coefficients (log odds)	p	Pseudo r^2	ΔAICc
DT + Ω_{low}	d.f. = 3			0.091	0.0
	Intercept	−0.70	0.0380		
	DT secondary	1.30	0.0001		
	Ω_{low}	−0.42	<0.0001		
DT + Ω_{low} + DT * Ω_{low}	d.f. = 4			0.093	1.0
	Intercept	−1.01	0.0321		
	DT secondary	1.68	0.0011		
	Ω_{low}	−0.25	0.1696		
	DT secondary * Ω_{low}	−0.20	0.3076		
DT + Ω_{low} + Q_{low}	d.f. = 4			0.092	1.7
	Intercept	−0.86	0.0474		
	DT secondary	1.29	0.0001		
	Ω_{low}	−0.35	0.0092		
	Q_{low}	−0.80	0.5544		
DT + Q_{low} + DT * Q_{low}	d.f. = 4			0.085	6.4
	Intercept	−1.56	<0.0001		
	DT secondary	1.16	0.0003		
	Q_{low}	−0.09	0.6672		
	DT secondary * Q_{low}	−0.33	0.1269		
DT + Q_{low}	d.f. = 3			0.081	6.6
	Intercept	−1.65	<0.0001		
	DT secondary	1.24	0.0001		
	Q_{low}	−0.39	<0.0001		

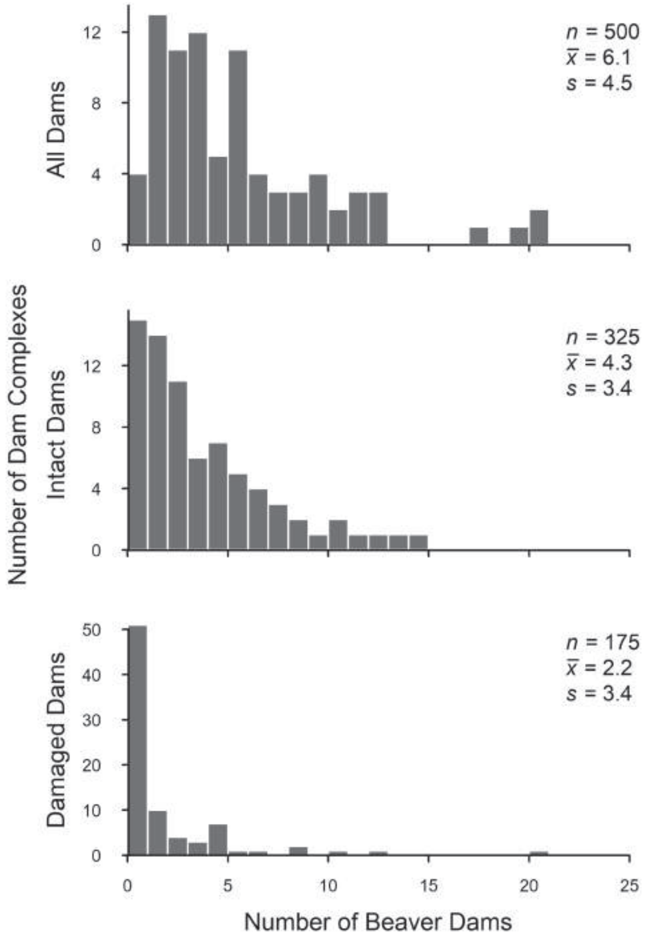

Figure 4. The number of dams per dam complex including all dams, intact dams, and damaged dams, where damaged dams are the combination of breached and blown-out dams. Data were collected in Utah and Idaho, USA between 11 May and 22 September 2016. The number of beaver dams (*n*), the average number of beaver dams per dam complex ($\overline{x}$), and standard deviation of the number of dams per complex (*s*) are reported for all dams, intact dams, and damaged dams.

Previous studies have indicated that beaver dam height varies with topography (Beedle, 1991; Gurnell, 1998), but few quantitative analyses exist to explain the nature of the stated relationships. We documented significant effects of slope, baseflow, and valley bottom width on dam height. Dam height increased with slope and decreased with stream power and valley bottom width. Though the effects of geomorphic variables were statistically significant, they described only a small proportion of dam height variability (Table 5), suggesting that variables not included in this study may be more important predictors of dam height. Specifically, our rapid field assessments did not measure channel width and depth, which are important variables for beaver dam site selection (McComb *et al.*, 1990; Dittbrenner *et al.*, 2018). These variables may also be important predictors of dam height because dams that do not expand out of the stream channel will be limited by channel dimensions and be more likely to breach or blow out because they experience greater stream power. However, channel width and depth are difficult to measure from 10m DEMs (the highest-resolution topography for our study sites) for small stream channels (Davies *et al.*, 2007).

Beaver dam complex structure and beaver dam height results describe conditions in the mountainous United States. Most study sites occurred on low-order (Strahler order 1–3) stream reaches with relatively narrow (<200m) valley bottoms. Beaver dams may be substantially longer and inundate much larger areas along streams with wider valley bottoms and low gradients (Ives, 1942; Hood and Bayley, 2008; Telegraph, 2010). In these settings, the large area of beaver ponds allows construction of a single beaver dam to support multiple lodges and food caches (Hood and Bayley, 2008). Therefore, fewer secondary dams may exist because construction of a single dam creates sufficient foraging range. In low-gradient systems, height differences between primary and secondary dams may also be less pronounced because even a short dam can inundate a large area. Additionally, dams must be longer to fully contain flow within the valley bottom, which increases the materials, effort, and time needed to construct tall dams.

The odds that a beaver dam was damaged were best explained by the HUC12 watershed the dam was located in. Statistical models relating geomorphic and hydrologic variables to damaged dams explained less than 10% of the variation in the data. The small proportion of variation explained by the reach and basin-scale variables (Table 7), and the large proportion of variation explained by HUC12 (17.8%), indicates that differences in physical and biological characteristics may be influencing dam persistence, but were not explicitly captured in our models. As with the dam height models, dependent variables used in logistic regression models did not represent channel geometry (e.g. channel width and channel depth), which can be an important factor for dam longevity (Gurnell, 1998; Demmer and Beschta, 2008; Persico and Meyer, 2009; Levine and Meyer, 2014; Pollock *et al.*, 2014). For example, unit stream power (i.e. stream power divided by channel width) is likely more representative of the forces acting on a beaver dam than total stream power because it is scaled by channel width (Pollock *et al.*, 2014; Macfarlane *et al.*, 2017). Quantifying unit stream power experienced by dams, and the impact of unit stream power on dam persistence, is a need that could be addressed by future research.

The HUC12 variable may also capture other variables that vary temporally, such as streamflow and climate conditions, and were not directly accounted for in our statistical models. Because each beaver dam was surveyed only once, we were not able to determine when dams were damaged, thus the variables used describe only static characteristics at each dam location and not dynamic variables (e.g. the actual flow and stream power experienced by a dam). Though Q_2 and Q_{low} were considered in regression models, these variables represented average annual values and not the actual values that occurred immediately preceding the dam blow-outs and breaches. Streamflow data preceding beaver dam survey dates were not available for streams where dams were surveyed. It is possible that certain basins, or streams, may have experienced flows that were higher or lower than the values used in regression models and resulted in damage (or lack thereof) to beaver dams. The low explanatory power of static variables used in these analyses indicates that dynamic variables, such as streamflow, may have greater effects on beaver dam persistence than the site at which a beaver dam is built. These results also imply that the date dams incur damage is important for identifying variables that may influence dam persistence.

Additionally, the probability of a dam incurring damage could be related to a number of other variables that were not collected during rapid field surveys. There is some evidence that the order in which a dam in a beaver dam complex is built, and the location of the dam in the complex, may affect its persistence, with the first dams built experiencing longer lives (Naiman *et al.*, 1988; Levine and Meyer, 2014). Dams that extend beyond the stream channel and onto the floodplain dissipate water out of the stream channel and thus reduce the force of water on the dam (Pollock *et al.*, 2014). Dams built on side channels will also experience less force from streamflow than dams built on the main channel. On beaver-altered streams many of these variables can be quite dynamic, with channels being created and disappearing as new dams are built and existing dams are breached. Our data, which were collected during a single year, do not capture this dynamism, which may be important for identifying when, and why, dams fail.

Conclusions

This work presents the largest sample size of dam heights for North American beaver (n =325) to date, improving empirical understanding of dam dimensions and the potential impacts of beaver dams. Dam type (primary/secondary) is identified as an important variable influencing dam height. The relative occurrence of primary and secondary dams is documented, with secondary dams occurring nearly six times more frequently than primary dams. These results indicate that beaver ecology, in addition to the geomorphology, hydrology, and ecology of stream reaches, influences the size and types of dams that are constructed.

Landscape variables that are important predictors of beaver dam capacity and beaver dam presence/absence explained only small amounts of variation (<3%) in beaver dam height and persistence. The low explanatory power of landscape variables indicates that channel characteristics (e.g. channel width and depth) at dam locations may exert more influence on dam height and persistence. Additionally, future research examining beaver dam persistence should include repeat dam surveys to identify the temporally variable factors (e.g. streamflow) that may affect the probability of beaver dams incurring damage.

Data presented herein, describing the height of beaver dams and the size of beaver dam complexes, provide important information for implementation and planning of beaver-based stream restoration efforts. The most important finding emphasizes that the height of beaver dams may be most influenced by ecological, rather than physical, constraints. Therefore, these data will be useful for preparing release sites for beaver reintroductions and conceptualizing how beaver colonization may alter stream reaches. We also point to the need for future studies to examine variables influencing dam height, dam persistence, and dam complex structure across a range of regions and with greater temporal detail.

Acknowledgements—We thank the US Forest Service and the Utah State University College of Research and Graduate Studies for funding this research. Additionally, we thank Wally Macfarlane for administrative support and expert opinion on beaver ecology, Matthew Meier and Creed Stevens for data collection efforts, Pete McHugh and Carl Saunders for assistance with statistical analyses, and Milada Majerova and Beth Neilson for providing data and expert advice. Comments from anonymous reviewers and Caroline Nash have improved the quality of this paper.

Conflict of Interest

The authors have no conflict of interest to declare.

Data Availability Statement

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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